NeuroImage **12,** 478–484 (2000)
doi:10.1006/nimg.2000.0635, available online at http://www.idealibrary.com on IDEAL®

RAPID COMMUNICATION

Representation of Manipulable Man-Made Objects in the Dorsal Stream

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Received March 6, 2000

We used fMRI to examine the neural response in frontal and parietal cortices associated with viewing and naming pictures of different categories of objects. Because tools are commonly associated with specific hand movements, we predicted that pictures of tools, but not other categories of objects, would elicit activity in regions of the brain that store information about motor-based properties. We found that viewing and naming pictures of tools selectively activated the left ventral premotor cortex (BA 6). Single-unit recording studies in monkeys have shown that neurons in the rostral part of the ventral premotor cortex (canonical F5 neurons) respond to the visual presentation of graspable objects, even in the absence of any subsequent motor activity. Thus, the left ventral premotor region that responded selectively to tools in the current study may be the human homolog of the monkey canonical F5 area. Viewing and naming tools also selectively activated the left posterior parietal cortex (BA 40). This response is similar to the firing of monkey anterior intraparietal neurons to the visual presentation of graspable objects. In humans and monkeys, there appears to be a close link between manipulable objects and information about the actions associated with their use. The selective activation of the left posterior parietal and left ventral premotor cortices by pictures of tools suggests that the ability to recognize and identify at least one category of objects (tools) may depend on activity in specific sites of the ventral and dorsal visual processing streams.

INTRODUCTION

We previously reported that, across multiple tasks, stimuli representing animals and tools (pictures and words) elicited category-related activity in ventral and lateral regions of the posterior temporal cortex (Chao *et al.*, 1999). Specifically, animals elicited bilateral activity in the lateral aspect of the fusiform gyrus and the posterior superior temporal sulcus, while tools elicited bilateral activity in the medial aspect of the fusiform gyrus and the middle temporal gyrus. These findings suggest that object knowledge may be represented in multiple cortical areas that store information about different object attributes such as form (in the ventral temporal cortex) and motion (in the lateral temporal cortex).

If the brain stores information about objects according to their features and attributes, then access to information about motor-based properties should be especially important for identifying manipulable man-made objects that are strongly associated with specific hand movements (i.e., tools).

In monkeys, there is evidence that a close link exists between common three-dimensional objects and the actions necessary to interact with them. Single-unit recording studies have identified neurons in the anterior intraparietal sulcus (AIP) (Sakata and Taira, 1994; Taira *et al.*, 1990) and a region in ventral premotor cortex area F5 (Rizzolatti *et al.*, 1988) that discharge during the execution of grasping movements. Because some of these neurons also discharge when the monkey merely looks at graspable objects (Murata *et al.*, 1997; Sakata *et al.*, 1995), it has been proposed that the actions associated with graspable objects are automatically evoked whenever the monkey sees these objects (Jeannerod *et al.*, 1995).

In humans, information about motor-based properties also seems to be represented in the parietal and premotor sites. For example, damage to these regions of the brain can disrupt knowledge about manipulable man-made objects as well as the actions necessary to interact with them. Patients with difficulty naming and retrieving information about tools often have left frontal lobe lesions, including the left premotor cortex (for review, see Gainotti *et al.*, 1995). Additionally, patients with left posterior parietal damage can have difficulty demonstrating the appropriate actions associated with the use of specific tools or utensils (i.e., ideational apraxia, De Renzi and Lucchelli, 1988; Ochipa *et al.*, 1989).

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Results from positron emission tomography (PET) studies of the intact human brain provide more supportive evidence for the role of the left premotor cortex in tool recognition. Several PET studies have found activity in the left premotor cortex when right-handed subjects named and retrieved information about tools (Grabowski *et al.*, 1998; Grafton *et al.*, 1997; Martin *et al.*, 1996). However, most of these studies compared tools to only one other category of object (e.g., Martin *et al.*, 1996 compared tools to animals; Grafton *et al.*, 1997 compared tools to fractal patterns). Thus, it is possible that the left premotor cortex responds to other categories of objects besides tools. Interestingly, Grabowski *et al.* (1998) reported that pictures of animals and famous faces also elicited activity in the left inferior prefrontal cortex, including the left premotor cortex. However, the face discrimination task that Grabowski *et al.* used as baseline, and the different presentation rates used for each object category, make it difficult to interpret these results.

The main aim of the present experiments was to re-evaluate the selectivity of the left premotor cortex for manipulable man-made objects. This was not possible in our previous study because we recorded only from posterior cortex (Chao *et al.*, 1999). We also investigated whether the presentation of a graspable object would activate the posterior parietal cortex in humans. Although previous neuroimaging studies have not reported tool-selective activity in the parietal cortex, results from the monkey and clinical studies discussed above suggest that the parietal cortex should also respond to the presentation of manipulable man-made objects. In the current studies, we used functional magnetic resonance imaging (fMRI) to examine the neural responses in frontal and parietal cortices associated with viewing and naming pictures of tools relative to other categories of animate and inanimate objects.

MATERIALS AND METHODS

Subjects

Ten neurologically normal, right-handed subjects participated in the study. All subjects gave written informed consent in accordance with procedures and protocols approved by the NIMH Institutional Review Board. Five subjects (1 male; mean age 26 $\pm$ 6.1 years) participated in Experiment 1 and five subjects (2 males; mean age 28 $\pm$ 4.8 years) participated in Experiment 2.

Experimental Design

The stimuli consisted of black-and-white photographs of tools, animals, faces, and houses. The control stimuli were phase-scrambled images of the same objects presented with the same timing. In Experiment 1 subjects were instructed to look carefully at pictures of tools, animals, faces, and houses. The pictures were presented at fixation at a rate of two per second. Experiment 1 utilized 1728 stimuli (432 different photographs per category). In Experiment 2 subjects were instructed to silently name pictures of tools and animals. The pictures were presented at fixation for 2 s. Experiment 2 utilized 360 stimuli (six exemplars of 30 namable animals and tools). The stimuli used in Experiment 2 were equated for word frequency and difficulty as determined by pilot testing (N = 10; mean voice onset time $\pm$ standard error; 946 $\pm$ 12 ms for animals; 966 $\pm$ 10 ms for tools; mean percentage correct $\pm$ SE: 96 $\pm$ 0.6% for animals; 95 $\pm$ 0.5% for tools). No stimuli were repeated in either experiment.

There were six imaging runs in each experiment. In Experiment 1, there were eight 18-second blocks with meaningful stimuli per run (two blocks for each stimulus type). In Experiment 2 there were six 21-s blocks with meaningful stimuli per run (three blocks each for animals and tools). The stimuli were blocked by category in both experiments. Blocks of control stimuli were presented at the beginning and end of each run and between blocks with meaningful stimuli. The order of blocks was counterbalanced across runs and subjects (additional details in Chao *et al.*, 1999).

Imaging

Twenty-two contiguous, 5-mm axial slices were obtained with a gradient echo, echo-planar imaging sequence (TR = 3 s, TE = 40 ms, flip angle = 90°, FOV = 24 cm, 64 $\times$ 64 pixels per inch matrix) on a 1.5 Tesla General Electric Signa scanner. During the same session as the fMRI scanning session, a structural MRI scan was obtained using a fast SPGR sequence (5-mm thick slices, TR = 13.9 ms, TE = 5.3 ms, flip angle = 20°, FOV = 24 cm, 256 $\times$ 256 matrix) that was coplanar with the functional EPI scans.

Image Analysis and Statistics

Data for each subject were analyzed separately using multiple regression (Friston *et al.*, 1995; Haxby *et al.*, in press). Movement between scans was corrected by aligning all EPI scans to a mean EPI scan using Automated Image Registration software (AIR; Woods *et al.*, 1993). Images were then smoothed in the axial plane using a Gaussian filter with a full width at half maximum of 1.2 voxels (4.5 mm). Changes in neural activity were modeled as a square wave step function coincident with the beginning and end of each stimulus block. These changes were decomposed into orthogonal contrasts: the differences between meaningful and control stimuli and the differences between tools and animals. In Experiment 1 there were additional contrasts to evaluate the differences between faces and houses, animals and faces, and tools and houses. The orthogo-

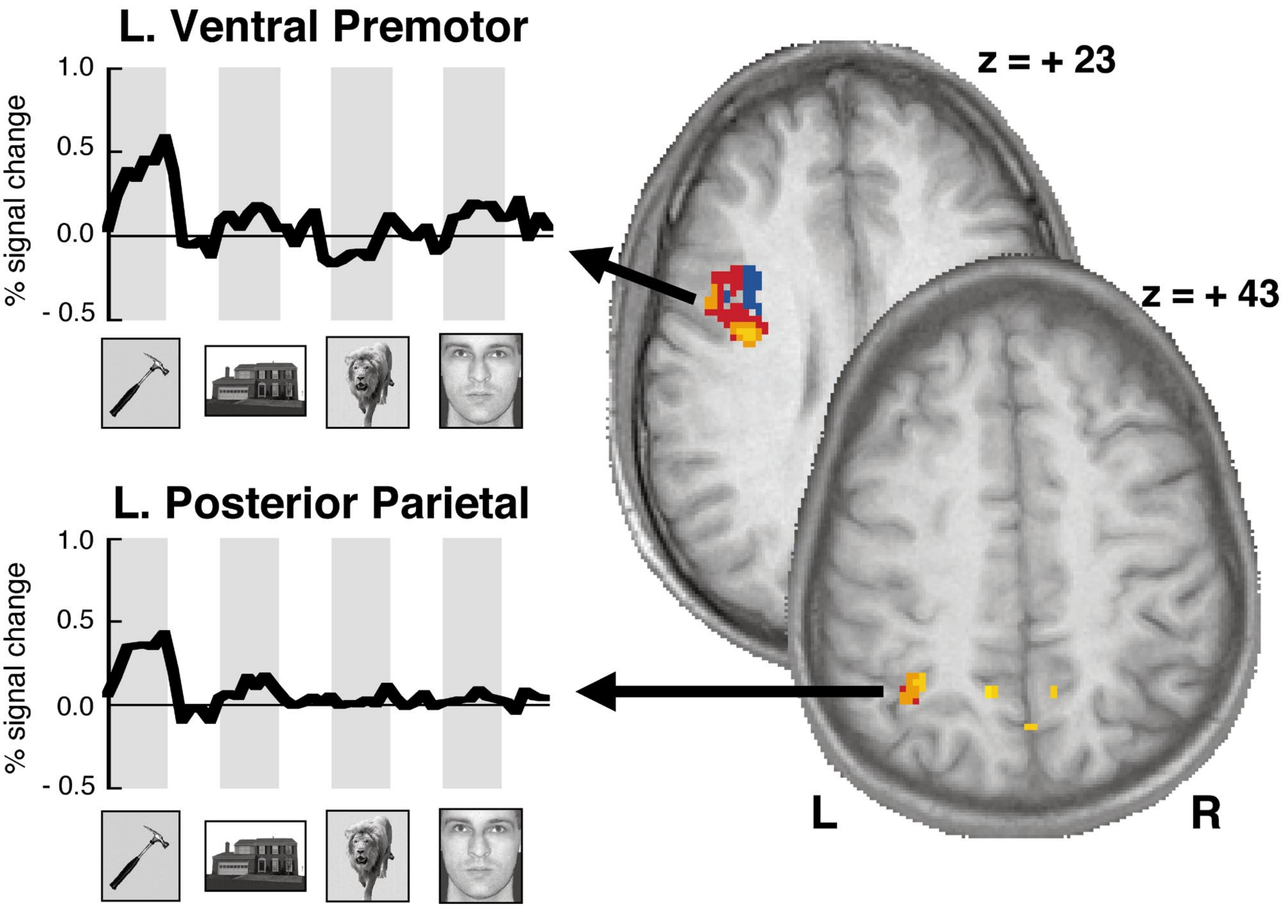

FIG. 1. Tool-selective activity in the left ventral premotor cortex and left posterior parietal cortex in a representative subject performing the viewing task (Experiment 1). The time series, averaged across subjects, for the two areas are presented on the left side of the figure. The gray bars indicate presentation of the meaningful stimuli (tools, houses, animals, and faces). The intervening white bars indicate presentation of the control stimuli (phase scrambled images of the objects). Note that tools elicited a significantly larger percent signal change compared to the other categories of objects in both the left ventral premotor and left posterior parietal cortices.

nal, square wave contrasts were convolved with a Gaussian model of hemodynamic response using experimentally derived estimates of lag (4.8 s) and dispersion (1.8 s). These convolved contrasts were the regressors of interest. Additional regressors of no interest were included to partial out variance due to differences in mean intensity between time series and linear changes in intensity within time series.

Voxels that showed a significant overall experimental effect ($Z > 3.09$, $P < 0.001$, for an omnibus test of the combined effect of the regressors of interest) and an overall increase in activity for meaningful stimuli (a positive regression weight for the contrast between meaningful and control stimuli) were selected for further analysis. Because the voxels were selected based on their overall response to objects, and not based on their differential response to tools, the voxels were not biased for any particular category. Next, clusters that showed a significantly greater response ($Z > 1.96$, $P < 0.05$, two-tailed, uncorrected for multiple comparisons) to tools relative to the other object categories were identified. Correction for multiple comparisons was achieved by an analysis of the spatial extent of clusters of voxels showing differential responses to tools and animals. Only clusters of seven or more contiguous voxels with $Z > 1.96$ were considered significant.

The anatomical locations of clusters of voxels showing significant differences between responses to tools and other stimuli were determined by superimposing their locations on coplanar high-resolution structural MRI scans. Voxels in significant clusters were used to determine the stereotaxic coordinates of the activations and to calculate mean time series for further statistical analysis. Identification of these voxels sometimes involved grouping neighboring but not contiguous significant clusters together or dividing a large cluster of contiguous voxels into different anatomical regions.

Location of each activation in the standard stereotaxic coordinates of the Talariach and Tounoux atlas

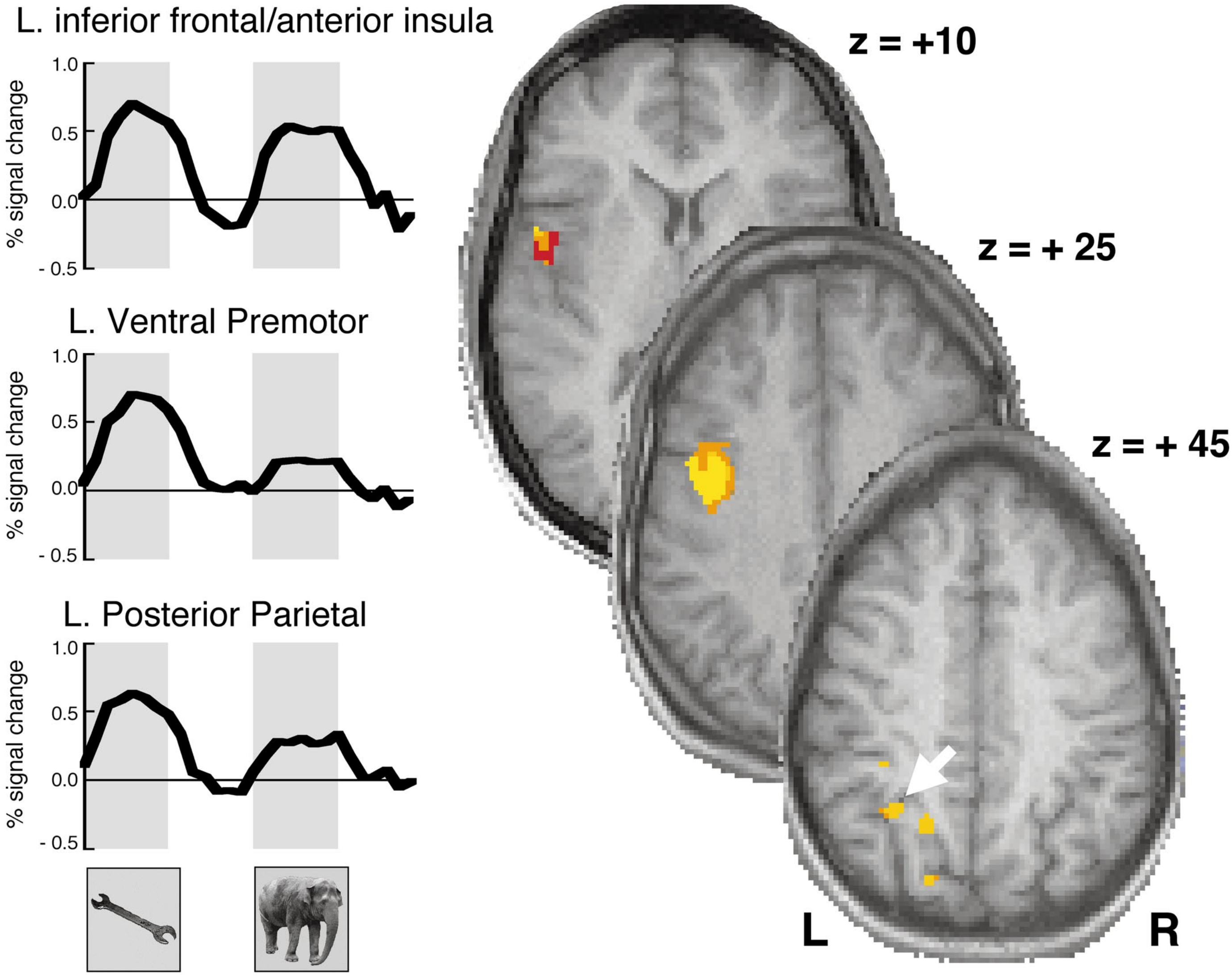

FIG. 2. Regions of significant activation in three selected slices for one subject performing the silent naming task (Experiment 2). The mean time series are presented on the left side of the figure. Note that the left inferior frontal/anterior insula responded equally to pictures of animals and tools. In contrast, tools elicited a significantly larger percent signal change than animals in both the left ventral premotor and left posterior parietal cortices.

(1988) was obtained. To correct for distortions the EPI data were registered to the coplanar structural MRI using a two-dimensional, rigid body alignment algorithm with AIR software. The coplanar structural MRI scans were registered to the high-resolution structural MRI scan, also using AIR software, and the registered statistical maps from the fMRI EPI data were similarly registered using the same resampling matrix. The high-resolution structural MRI was then resampled into the standard stereotaxic brain coordinates of the Talairach and Tournoux atlas (1988) and the registered fMRI statistical maps were shadowed into the same coordinate space using SPM96b software.

For each subject and each activation, a mean time series, averaged across activated voxels and across repetitions of blocks with the same stimulus type, was calculated. For Experiment 1, each mean time series consisted of 48 time points (six time points per stimulus type and six time points for control blocks following each stimulus type). For Experiment 2, each mean time series consisted of 28 time points (seven time points per stimulus type and per control block). Each time point in these mean time series represents the average of six experimental runs.

Multiple regression was used to measure the size of the response to each meaningful stimulus condition as a percent signal change above activity elicited by the phase-scrambled control. Measures of percent response were then analyzed with a repeated-measures analysis of variance.

RESULTS

Behavioral data collected after scanning documented that the animal and tool stimuli used in Experiment 2 were equated for naming time (mean voice on-set time ± SE, 920 ± 12.1 ms; 948 ± 12.5 ms) and accuracy (percent correct ± SE, 96 ± 0.7%; 95 ± 0.9%).

In Experiment 1, three of five subjects showed significant activations in the left ventral premotor cortex (BA 6) and four of five subjects showed significant activations in the left posterior inferior parietal cortex, including the intraparietal sulcus (BA 40). There were significant effects of stimulus type in both the left ventral premotor cortex ($P = 0.03$) and the left posterior inferior parietal cortex ($P < 0.0005$). Within each of these regions, tools elicited a significantly stronger response than each of the other object categories ($P < 0.05$ to $P < 0.006$; see Fig. 1).

In Experiment 2, all five subjects showed significant activations in the left ventral premotor cortex while three of five subjects showed significant activations in the left posterior inferior parietal cortex, centered in the intraparietal sulcus. Again, there were significant effects of stimulus type in the left ventral premotor cortex ($P = 0.01$) and the left posterior inferior parietal cortex ($P < 0.005$), with pictures of tools eliciting a stronger response in both regions. In addition, significant activity was found in the left inferior prefrontal cortex/anterior insula (BA 44). However, animal and tool naming produced similar amounts of activity in this area (see Fig. 2). The location and size of all activations in Experiments 1 and 2 are provided in Table 1.

DISCUSSION

Our ability to identify different objects may depend on the activation of stored information about the sensory- and motor-based attributes that define an object and distinguish it from other members of the same category (Martin *et al.*, 2000). Results from our previous experiment (Chao *et al.*, 1999) suggest that pictures of tools elicit activity in a distributed network of cortical regions that prominently include the ventral and lateral regions of the posterior temporal cortex. Results from the current study extend this network to include other areas of the brain.

Relative to viewing and naming pictures of multiple categories of objects, the left ventral premotor cortex responded selectively to pictures of tools. Interestingly, previous PET studies of imagined right hand movements have also reported activity in a similar region of the left ventral premotor cortex (Decety *et al.*, 1994; Grafton *et al.*, 1996; Stephan *et al.*, 1995). This suggests that the current left ventral premotor activation may be related to the retrieval of information about right-hand movements associated with the use of manipulable man-made objects.

Single-unit recordings in monkeys suggest that information about graspable objects is represented in a network of regions including area F5 in ventral premotor cortex (Rizzolatti *et al.*, 1988). There are two types of neurons in area F5: canonical neurons and mirror neurons (Rizzolatti and Fadiga, 1998). Canonical neurons, located inside the arcuate sulcus, respond to the visual presentation of graspable objects. For this reason, it has been proposed that canonical neurons play a role in object-to-hand movement transformations (Jeannerod *et al.*, 1995). A similar effect was noted in the current study. Viewing and naming pictures of tools selectively activated the left ventral premotor cortex. These results suggest that, in the human brain, the homolog of the monkey canonical F5 area may be located in the left ventral premotor cortex.

In contrast, mirror neurons, located on the cortical convexity of the arcuate sulcus, respond when the monkey performs an action and when the monkey observes another individual performing a similar action (Rizzolatti *et al.*, 1996). For this reason, it has been proposed that mirror neurons play a role in the imitation and understanding of actions (Jeannerod, 1994; Rizzolatti *et al.*, 1996). A recent fMRI study by Iacoboni *et al.* (1999) reported activity in a region of the left frontal operculum/Broca's area (BA 44) when human subjects observed others performing finger movements. Importantly, this area became more active when subjects executed the finger movements, and most active when subjects both observed and executed the finger movements (i.e., during imitation). Thus, these findings suggest that the left frontal operculum/Broca's area (BA 44) may be the human homolog of the monkey mirror F5 area, in accordance with a proposal by Rizzolatti and Arbib (1998).

It is interesting to note that in the monkey brain, mirror neurons are adjacent to canonical neurons and both populations of neurons are located in BA 6. In contrast, the putative human homolog of mirror F5 is located in BA 44 while the putative human homolog of canonical F5 is located in BA 6. This difference in functional neuroanatomy between monkey mirror and canonical F5 and the human homolog of these areas may have occurred as a result of the expansion of the prefrontal cortex over the course of primate brain evolution. Nevertheless, there appears to be a close homology between the functional organization of certain parts of the prefrontal and premotor cortices in humans and monkeys.

We also found significant activity in the left inferior prefrontal cortex/anterior insula. Recent neuroimaging studies have provided evidence that a similar region of the left inferior frontal cortex is active during a wide range of language tasks (for review, see Poldrack *et al.*, 1999). It is likely that this activation is related to lexical search and retrieval and phonological processing for the following reasons: First, this region of the

TABLE 1

Dorsal Regions Showing Preferential Response to Tools

	Hemisphere	N	Volume (cm^3)	Talairach coordinates		
				x	y	z
Experiment 1 (Viewing)						
Ventral premotor	Left	3	2.3 ± 0.8	−42 ± 7	6 ± 1	23 ± 5
Posterior parietal	Left	4	2.6 ± 0.5	−32 ± 5	−47 ± 9	42 ± 6
Experiment 2 (Naming)						
Inferior frontal/insula	Left	5	3.5 ± 2.6	−30 ± 7	17 ± 3	9 ± 2
Ventral premotor	Left	5	1.9 ± 0.8	−50 ± 6	3 ± 4	25 ± 8
Posterior parietal	Left	3	0.8 ± 0.1	−30 ± 3	−39 ± 2	47 ± 1

Note. Volumes were calculated before spatial normalization. Coordinates refer to the Talairach and Tournoux brain atlas. All volumes and coordinates are mean ± SD. N indicates the number of subjects (of 5) who showed significant category-related activation ($P < 0.05$).

prefrontal cortex was only active in Experiment 2, where subjects had to explicitly name the stimuli. Second, this region of the brain responded equally to pictures of animals and tools. Finally, the Talairach coordinates of this activation were close to the coordinates of other left prefrontal activations reported in linguistic processing tasks (e.g., Bookheimer *et al.*, 1995; Braver *et al.*, 1997; Fiez *et al.*, 1995; Martin *et al.*, 1996; Rumsey *et al.*, 1997).

While the current left inferior prefrontal cortex/anterior insula activation is also in BA 44, it is located in a more medial area of BA 44 than that reported by Iacoboni *et al.*, (1999). Because we only examined the neural response associated with viewing and naming pictures of objects, the relationship between the region of BA 44 that responds during lexical selection and retrieval and the region that responds when viewing hand and finger movements remains to be determined.

Viewing and naming pictures of tools, but not other categories of objects, also activated the left posterior parietal cortex. A recent fMRI study of object grasping reported activity in a similar region of the left posterior parietal cortex (−40, −40, 40; Binkofski *et al.*, 1999). Moreover, humans with left posterior parietal lesions, including the intraparietal sulcus, often have difficulty controlling hand and finger movements during grasping (Binkofski *et al.*, 1998; Perenin and Vighetto, 1988). Together, these findings suggest that the tool-selective response in the left posterior parietal cortex may be related to the retrieval of information about hand and finger movements associated with the use of manipulable man-made objects.

Goodale and Milner (1992) have proposed that the parietal cortex provides information necessary for the control of object-directed action. Our data suggest that the left posterior parietal cortex also provides motor-based information important for recognizing manipulable man-made objects. Thus, our ability to recognize certain classes of objects (e.g., tools) may depend on the integration of information from both the ventral and dorsal streams.

In conclusion, results from this and our previous study (Chao *et al.*, 1999) suggest that, in right-handed individuals, regions of the fusiform gyrus, middle temporal gyrus, left posterior parietal cortex, and left ventral premotor cortex form a network that links information about the visual features and attributes that characterize objects as distinct tools with the appropriate hand and finger movements necessary for using them. These findings suggest that this network of ventral and dorsal sites is active whenever we recognize and identify manipulable man-made objects.

REFERENCES

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., and Freund, H. J. 1999. A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Exp. Brain Res.* **128:** 210–213.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., and Freund, H. J. 1998. Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology* **50:** 1253–1259.

Bookheimer, S. Y., Zeffiro, T. A., Blaxton, T., Gaillard, W., and Theodore, W. 1995. Regional cerebral blood flow during object naming and word reading. *Hum. Brain Map.* **3:** 93–106.

Braver, T. S., Cohen, J. D., Nystrom, L. E., Jonides, J., Smith, E. E., and Noll, D. C. 1997. A parametric study of prefrontal cortex involvement in human working memory. *NeuroImage* **5:** 49–62.

Chao, L. L., Haxby, J. V., and Martin, A. 1999. Attribute-based neural substrates in posterior temporal cortex for perceiving and knowing about objects. *Nature Neurosci.* **2:** 913–919.

De Renzi, E., and Lucchelli, F. 1988. Ideational apraxia. *Brain* **111:** 1173–1185.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J. C., and Fazio, F. 1994. Mapping motor representations with positron emission tomography. *Nature* **371:** 600–602.

Fiez, J. A., Riachle, M. E., Miezin, F. M., Petersen, S. E., Tallal, P., and Katz, W. F. 1995. PET studies of auditory and phonological processing: Effects of stimulus characteristics and task design. *J. Cogn. Neurosci.* **7:** 357–375.

Friston, K. J., Holmes, A. P., Poline, J. B., Grasby, P. J., Williams, C. R., and Frackowiak, R. S. J. 1995. Analysis of fMRI time-series revisited. *NeuroImage* **2:** 45–53.

Gainotti, G., Silveri, M. C., Daniele, A., and Giustolisi, L. 1995. Neuroanatomical correlates of category-specific impairments: A critical survey. *Memory* **3/4:** 247–264.

Goodale, M. A., and Milner, A. D. 1992. Separate visual pathway for perception and action. *Trends Neurosci.* **15:** 20–25.

Grabowski, T. J., Damasio, H., and Damasio, A. R. 1998. Premotor and prefrontal correlates of category-related lexical retrieval. *NeuroImage* **7:** 232–243.

Grafton, S. T., Arbib, M. A., Fadiga, L., and Rizzolatti, G. 1996. Location of grasp representations in humans by position emission tomography: 2. Observation compared with imagination. *Exp. Brain Res.* **112:** 103–111.

Grafton, S. T., Fadiga, L., Arbib, M. A., and Rizzolatti, G. 1997. Premotor cortex activation during observation and naming of familiar tools. *NeuroImage* **6:** 231–236.

Haxby, J. V., Maisog, J. M., and Courtney, S. M. 2000. Multiple regression analysis of effects of interest in fMRI time series. In *Mapping and Modeling the Human Brain* (J. Lancaster, P. Fox, and K. Friston, Eds.) Wiley, New York, in press.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., and Rizzolatti, G. 1999. Cortical mechanisms of human imitation. *Science* **286:** 2526–2528.

Jeannerod, M. 1994. The representing brain: Neural correlates of motor intention and imagery. *Behav. Brain Sci.* **17:** 187–245.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., and Sakata, H. 1995. Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends Neurosci.* **18:** 314–320.

Martin, A., Ungerleider, L. G., and Haxby, J. V. 2000. Category-specificity and the brain: The sensory-motor model of semantic representations of objects. In *The Cognitive Neurosciences* (M. S. Gazzaniga, Ed.) pp. 1023–1036. MIT Press, Cambridge, MA.

Martin, A., Wiggs, C. L., Ungerleider, L. G., and Haxby, J. V. 1996. Neural correlates of category-specific knowledge. *Nature* **379:** 649–652.

Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., and Rizzolatti, G. 1997. Object representation in the ventral premotor cortex (area F5) of the monkey. *J. Neurophysiol.* **78:** 2226–2230.

Ochipa, C., Rothi, L. J. G., and Heilman, K. M. 1989. Ideational apraxia: A deficit in tool selection and use. *Ann. Neurol.* **25:** 190–193.

Perenin, M. T., and Vighetto, A. 1988. Optic ataxia: Specific disruption in visuomotor mechanisms. *Brain* **111:** 643–674.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., and Gabrieli, J. D. E. 1999. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage* **10:** 15–35.

Rizzolatti, C., Camarada, R., Fogassi, L., Gentilucci, M., Luppion, G., and Matelli, M. 1988. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp. Brain Res.* **71:** 491–507.

Rizzolatti, G., and Arbib, M. A. 1998. Language within our grasp. *Trends Neurosci.* **21:** 188–194.

Rizzolatti, G., and Fadiga, L. 1998. Grasping objects and grasping action meanings: The dual role of monkey rostroventral premotor cortex (area F5). *Novart FDN Symp.* **218:** 81–103.

Rizzolatti, G., Fadiga, L., Fogassi, L., and Gallese, V. 1996. Premotor cortex and the recognition of motor actions. *Cog. Brain Res.* **3:** 131–141.

Rumsey, J. M., Horwitz, B., Donohue, B. C., Nace, K., Maisog, J. M., and Andreason, P. 1997. Phonological and orthographic components of word recognition: A PET-rCBF study. *Brain* **120:** 739–759.

Sakata, H., and Taira, M. 1994. Parietal control of hand action. *Curr. Opin. Neurobiol.* **4:** 847–856.

Sakata, H., Taira, M., Murata, A., and Mine, S. 1995. Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cereb. Cortex* **5:** 429–438.

Stephan, K. M., Fink, G. R., Passingham, R. E., Silbersweig, D., Ceballos-Baumann, A. O., Firth, C. D., and Frackowiak, R. S. J. 1995. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J. Neurophysiol.* **73:** 373–386.

Taira, M., Mine, S., Georgopoulos, A. P., Murata, A., and Sakata, H. 1990. Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Exp. Brain Res.* **83:** 29–36.

Talairach, J., and Tournoux, P. 1988. *Co-planar Stereotaxic Atlas of the Human Brain.* Thieme, New York.

Woods, R. P., Mazziotta, J. C., and Cherry, S. R. 1993. MRI-PET registration with an automated algorithm. *J. Comput. Assist. Tomogr.* **17:** 536–546.